

BREEDING BIOLOGY AND NEST SITE CHARACTERISTICS OF THE BICOLORED HAWK IN GUATEMALA

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ABSTRACT.—We studied the breeding biology of the Bicolored Hawk (*Accipiter bicolor*) in the forest of Tikal National Park of northeastern Guatemala from 1991 to 1994. Bicolored Hawks are year-round residents and establish nesting territories during the breeding season, which coincides with the late dry season and beginning of the wet season. Nest building and courtship spanned 92 days. We documented 17 nesting attempts from February to July 1991–1994. Egg-laying began in April and May, with 36 eggs laid in 15 nests for an average clutch size of 2.4 (range 1–3 eggs). We documented one renesting after failure of the first clutch. Incubation was approximately 35 days ($n = 5$ clutches). Young hatched asynchronously with a light pinkish natal down. Of 36 eggs laid, 64% hatched. Nearly all hatching occurred during May except one renesting, from which one young hatched on 26 June 1994. Young departed from the nest tree at 30–36 days of age and 100% of the nestlings fledged; thus a total of 1.4 young fledged per breeding attempt and overall nest success was 76%. Most reproductive losses occurred during the incubation period. We found addled eggs in 2 nests and egg predation and nestling predation at 1 nest each. Bicolored Hawk nests averaged 22 m above the ground in living trees 75 cm in diameter. All nests were stick nests, averaging 51 × 44 cm exterior diameter, 26 cm exterior depth, and 3.6 cm interior depth. The Bicolored Hawk diet of 173 identified prey was composed almost exclusively of birds (95%) with relatively few mammals (3%) or reptiles (2%) taken. Received 3 June 1999, accepted 26 Jan. 2000.

Among Neotropical birds, raptors are one of the least studied groups and relatively little is known about their breeding biology (Thiollay 1985, Bierregaard 1995). Raptors in tropical environments tend to have longer breeding seasons and lower reproductive rates than their temperate counterparts (Newton 1979, Mader 1982, Delannoy and Cruz 1988, Thorstrom 1993). Tropical raptors are also known to lay replacement clutches after losing eggs or young, which rarely occurs in temperate areas (Newton 1979, Mader 1982, Delannoy and Cruz 1988).

The widespread genus *Accipiter* includes seven small to medium-sized hawks confined to the mainland Neotropics. One widely distributed Neotropical accipiter is the Bicolored Hawk (*Accipiter bicolor*), member of a super-species that includes the Cooper's Hawk (*A. cooperi*), Gundlach's Hawk (*A. gundlachi*), and Chilean Hawk (*A. chilensis*; del Hoyo et al. 1994).

The Bicolored Hawk is widespread but rarely observed, ranging from northern Argentina to southern Mexico. It mainly inhabits lowland and subtropical forests but also reach-

es the lower limit of the temperate zone around 2500 m in the Andes (del Hoyo 1994, Fjeldså and Krabbe 1990). During raptor surveys in and around Tikal National Park, a lowland tropical forest of northeastern Guatemala, this species was rarely detected in visual or aural censuses (Whitacre et al. 1991, Jones and Sutter 1992). Smithe (1966) reported Bicolored Hawks as "uncommon but not rare" at Tikal National Park, while Beavers (1992) coded it as rare.

Little is known about the breeding biology of the Bicolored Hawk. Unlike Temperate raptors, it is very difficult to detect because it is secretive, inconspicuous, its vocalizations are weak even during the breeding period, and pairs do not appear to perform courtship flights over the nest area (Palmer 1988). Mader (1981) reported one successful breeding attempt that fledged two young and one nest built and then abandoned, both during the wet season (April and May) in Venezuela. Our study summarizes information collected during four years on breeding biology, behavior, and nests of this inconspicuous forest raptor.

STUDY AREA AND METHODS

This study was conducted in Tikal National Park (17° 13' N, 89° 36' W) which encompassed 576 km². This park is in a lowland, dry, semi-deciduous, tropical forest with an annual mean rainfall of 1348 mm (based on 1989–1992 data). Several forest types, which occur

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along topographical drainage, soil type, and moisture gradients, have been described for the park (Schulze and Whitacre 1999). Two extremes of this continuum are upland or high-ground forests (tall, semi-evergreen forests on well-drained shallow soils) and "bajo" forests (low in stature, with open canopy and dense understory, occurring in low-lying sites of deep clay-rich soils, subject to seasonal flooding and drought). Between these two readily distinguishable forest types is a transitional zone at the base of hills or on slopes from uplands to low lying basins.

Paired birds and nests were located opportunistically during foot searches for forest-falcons and other potentially nesting raptors. One nest was located from a trapped and radio-tagged male. Nest observations were made from the ground and from tree platforms with 8× and 10× binoculars at distances of 35–50 m. We observed each nest site 5–6 hours per observation period and rotated between mornings and afternoons every three to four days. Nest measurements were taken on accessible nests. Nest height was measured in plumb-line distance from the nest to ground level and nest tree diameter was measured at breast height. The incubation period was calculated as the time (days) from laying of last egg (after clutch completion) to hatching of the last egg. We measured egg dimensions to the nearest 0.1 mm with vernier calipers and determined egg mass and body mass of adults with 100 g and 500 g Pesola spring scales to the nearest 1 g and 5 g, respectively. Bicolored Hawks were trapped with bal-chattris and a noose carpet placed near or on the nest during incubation (Newton 1986, Thorstrom 1996). Six birds were color banded for identification.

For our analyses reproductive variables were defined as territorial pair-years (territories where pairs bred or maintained a territory but did not breed; several nests were constructed but no eggs were laid), nesting (breeding) attempt (nests that contained at least one egg), eggs laid (number of observable eggs laid in accessible nests), mean clutch size (number of observable eggs laid per nesting attempt), eggs hatched (number of eggs hatched), young fledged (number of young surviving to fledging), productivity (number of young fledged per nesting attempt), overall productivity (number of young fledged per territorial pair), and nest success (number of total nesting attempts that fledged at least one young).

Breeding density was determined by two methods. We calculated the mean neighbor distance between nests following Selås (1998) and determined the radius from this measurement. The area of a nesting territory was calculated as $A = \pi r^2 \times 1.158$, where 1.158 is a constant that included the area of non-overlap between neighboring territories (Brown 1975). Breeding density was also calculated from the polygon area that enclosed all nests located and might include unused habitat. The polygon was produced by connecting the outermost nests and then extending the sides by half the mean minimum internest distance (Berkelman 1996). The demarcated area was calculated by CAMRIS GIS

(Ecological Consulting, Inc., Portland, Oregon). Except where stated, measures give are means \pm SD.

RESULTS

We located 3 nest sites in 1991, 2 in 1992, 1 in 1993, and 1 in 1994 for a total of 7 nesting territories.

Courtship behavior and nest building.—Courtship activities occurred from February to April. No territorial or aerial flights were observed in this species. Courtship behavior consisted of vocalizations, nest building activities, courtship feedings, copulations, and nest defense. Both adults took part in nest construction. The earliest nest building activity was observed on 5 February 1992. In 1991, during 100 h of observation at three nests, we observed deliveries of 81 dry sticks with males contributing 41 (50.6%) and female 40 (49.4%). Most nest building and copulations occurred 06:00–07:00. The earliest copulation was observed on 28 February 1992, approximately 5 weeks before egg laying. Copulations usually occurred after courtship feedings, and occasionally after nest building activities. From 05:30 to 06:30, one pair was observed copulating 3 times. Nest building and courtship spanned 92 days (5 February to 8 May) and peaked in mid-March.

Nest characteristics.—Nests were built in trees on single or forked branches or on hanging vines. Birds collected dry sticks and twigs from trees within 20–50 m of the nest site. Several nests contained dried leaves as nesting material in the nest cup. Nearly all pairs built new nests every year and the average distance between alternate nests in a given territory in successive years was 94 ± 57 m (range 30–200 m, $n = 10$). Two nests were used by the same banded pairs for 2 years (1992, 1993) and one for 3 consecutive years (1991–1993). In 1994, one pair reconstructed and occupied the nest of a Crane Hawk (*Geranospiza caerulescens*) built in 1993. We documented only one renesting effort after first clutch loss and that pair constructed a new nest in 3 weeks from 5–23 May 1994.

Bicolored Hawk nests averaged 21.7 m above the ground in live trees averaging 74.6 cm dbh (Table 1). Thirteen nests were supported by branches and two were supported by hanging vines. Forty percent ($n = 6$) of nest trees were situated in bajo forest, 53.3%

TABLE 1. Bicolored Hawk nest site characteristics.

Nest site characteristics	Mean	SD	Range	n
Nest height (m)	21.7	2.3	17.2–27	15
Nest tree diameter (cm)	74.6	16.9	58.2–124	15
Nest width (cm)	43.6	12.8	15–63	12
Nest length (cm)	51.3	15.8	30–97	15
Nest depth exterior (cm)	26.5	11.7	12–30	14
Nest depth interior (cm)	3.6	2.1	2–9	15
Nest support branch diameter (cm)	9.4	4.8	4–15	11
Nest distance from trunk (m)	3.5	3.7	0–9	11

($n = 8$) in transitional forest, and 6.7% ($n = 1$) in upland forests. Fifteen of 19 nests were constructed in different trees of 6 species: 33.3% (5) were in *Brosimum alicastrum*, 26.7% (4) in *Swietenia macrophylla*, 13.3% (2) in *Vitex gaumeri*, 13.3% (2) in *Lonchocarpus castilloi*, 6.7% (1) in *Pouteria amygdalina*, and 6.7% (1) in *Manilkara zapota*.

Egg laying, incubation and hatching.—By mid-April, females remained near the nest sites and were mostly inactive. We observed two males (one banded and one unbanded) copulating with the same banded female at one nest site in 1993 prior to egg laying. After egg laying, the unbanded male disappeared, and the banded male attended the female and nest site through a successful breeding attempt. Laying of first clutches spanned 36 days (2 April to 8 May). Earliest recorded laying dates were 4 April 1991, 2 April 1992, 6 April 1993, and 2 April 1994. First clutches averaged 11 April \pm 10 days (SD; $n = 15$ clutches) for the four years (range 2 April to 8 May). The most common clutch size was three ($n = 8$), followed by clutches of two ($n = 5$), and there were two one-egg clutches, one of which was a replacement clutch, for a mean clutch size of 2.4 ± 0.7 . We suspect that full incubation began when the penultimate egg was laid. Mean dimensions of 14 Bicolored Hawk eggs were 47.1 ± 1.1 mm (44.9–49.0 mm) by 36.5 ± 1.1 mm (35.0–38.6 mm; see Thorstrom and Kiff 1999). Average egg mass was 33.5 ± 3.5 g (28.0–38.0 g, $n = 14$ eggs), 7.1% of the female's body mass (average female body mass was 470 g; $n = 4$), and 21.3% of her mass for a clutch of three eggs.

Females performed most of the incubation, and the males provided food to the female and nestlings. Males gave sharp *kek* calls upon ar-

rival to the nest while females solicited food with a nasal *wreh* vocalization. Occasionally males tried to incubate after delivering food to the female away from the nest, but incubation duration of males ranged from 30 seconds to 5 min at which time females returned to the nest and males moved off. The incubation period from laying to hatching of the penultimate egg was 34 ± 1 days ($n = 5$ clutches). Hatching was asynchronous, spanning 1–3 days. Nearly all hatching occurred during May except for the renesting, from which one young hatched on 26 June 1994 (Table 2). Hatching for all years peaked on 16 May \pm 5 days and spanned 14 days (9–23 May, $n = 10$ nests).

Development of young.—One week prior to fledging, young moved around in the nest and onto nearby limbs. Sometimes they were located 3–4 m above and beyond the nest in branches, occasionally fluttering, hopping, and flying back to the nest.

Fledging period and natal dispersal.—Young fledged (took their first flight from the nest tree) 30–36 days after hatching. Males appeared to fledge earlier (30–32 days; $n = 3$) than females (34–36 days; $n = 2$). Fledging spanned nearly 7 weeks, from the first week of June to late July. After fledging, young remained in the nest area and returned to the nest frequently. Adults continued to deliver food to the young during the first few weeks after fledging. When young were capable of handling prey they fed away from the nest and their siblings. Young constantly solicited food and mobbed adults when they entered the nest area.

At one nest site, two telemetered young males probably dispersed on 25 August 1991, when we lost radio contact, 9 weeks after fledging (98 days of age). These two young

TABLE 2. Nestling development and behavior ($n = 2$ males in 1991).

Age	Measurements (mm)	Weight (g)	Physical characteristics and behavior
Hatch (day 0)		25–28	Light pinkish down, black beaks, white-gray nails and pale yellow ceres
Week 1	Body length 140, wing 90	120	Natal down white, cere yellowish orange and egg tooth disappearing
Week 2	Body length 220, wing 170	200–220	Young with primaries emerging and parasitic fly larvae attached to wing blood feathers
Week 3	Body length 230, wing 225, tail 40		Active in nest calling and moving around
Week 4	Body length 305, wing 153, tail 80		Very active and moving outside of the nest on branches
Week 5			

ranged up to 400 m from their nest tree during the post-fledgling period. Two other young were radio-tagged to monitor natal dispersal but they were out of the range of our equipment by four and five weeks, and the lack of roads made coverage of their movements difficult.

Productivity and reproductive success.—Seven territorial pairs were studied for a total of 21 territorial pair-years from 1991 through 1994 (Table 3). In these 21 pair-years, 19 nests were built and 17 nesting attempts were observed (eggs laid). Clutch size was documented for 15 nesting efforts, totaling 36 eggs ($\bar{x} = 2.4$ eggs). In 10 fully documented nests containing 27 eggs, 20 eggs (74%) hatched and all of the hatched young fledged. In total, 24 young (100%) fledged from 13 breeding attempts, for a productivity of 1.8 young fledged per successful attempt. Overall productivity was 1.1 (24/21) young per territorial pair-year. Nest success for the four years of the study was 76% (13/17).

In the 17 nesting attempts, 3 nest failures occurred during incubation and 1 during the nestling stage. The causes for nest failure were added eggs ($n = 2$ nests) and predation (possibly mammalian) on eggs or nestlings ($n = 2$ nests).

The 7 territorial pairs we documented from 1991 to 1994 fledged 24 young. One pair raised young in each of the four years of the study, producing 33% ($n = 8$ young) of the total young fledged. This pair used the same nest in three successive years (1991–1993) and moved to another nest site 35 m away in 1994.

Few mortalities were observed in either young or adults. One adult female apparently drowned while attempting to drink from or capture prey near a man-made well. We suspect that overall adult mortality for the Bicolored Hawk is low. For example, one adult female banded in 1991 was still on her territory in 1994. No immature plumaged young was detected on nesting territories.

Breeding density.—Using the mean distance between neighboring nests we calculated that a nesting territory occupied 4.0 km² for a total of 23.8 km² for six contiguous territories. The six nesting territories were enclosed within a 33.4 km² polygon resulting in a breeding territory of 5.5 km². This estimate

TABLE 3. Annual reproductive success of Bicolored Hawks during the breeding season 1991 to 1994 at Tikal National Park, Guatemala.

Year	Territorial pair-years	Nesting attempts ^a	Eggs laid (nests)	Mean clutch size	Eggs hatched (%) ^b	Young fledged (%) ^b	Productivity	Overall productivity	Successful nests n (%)
1991	3	3	9 (3)	3.0	4 (44)	3 (75)	1.0	1.0	2 (66)
1992	5	5	9 (4)	2.3	8 (89)	10 (100)	2.0	2.0	5 (100)
1993	6	4	8 (3)	2.7	5 (63)	5 (100)	1.3	0.8	3 (75)
1994	7	5	10 (5)	2.0	6 (60)	6 (100)	1.2	1.0	3 (60)
Total	21	17	36 (15)	2.4	23 (64)	24 (100)	1.4	1.1	13 (76)

^a Number of nests with egg laid.

^b Two nests were discovered with nestlings before we made an egg count.

also may have included parts of one or two territories for which nests were not found but contained birds.

Food habits.—From 1991–1994, we recorded 272 Bicolored Hawk prey items at Tikal, mainly those brought to nests; 173 were identified at least to class. Birds comprised 95% (164) of identified prey, mammals (bats and rat-sized rodents) 3% (6), and reptiles (lizards) 2% (3). Ninety-nine prey items were unidentified to species; these were often plucked and partly eaten before delivery to the nest, rendering their identification impossible. During the breeding season, adult males were observed taking birds ranging from euphonias (*Euphonia* spp.) and greenlets (*Hylophilus* spp.; 8–16 g) to motmots (*Momotus* spp.; 133 g), while adult females were observed to take ant-tanagers (*Habia* spp.; 31–38 g), toucanets (*Aulacorhynchus* spp.; 150 g) and puffbirds (*Bucco* spp.; 96 g). Wintering Wood Thrushes (*Hylocichla mustelina*; 48 g) and woodcreepers (*Dendrocincla* spp.; 30–80 g) made up the bulk of the species taken by both sexes (weights from Dunning 1993).

DISCUSSION

Breeding cycle.—The courtship and territorial behavior of the Bicolored Hawk appears to differ from other *Accipiter* hawks (Newton 1979, Brown and Amadon 1989). Although soaring has been reported for this species (Fjeldså and Krabbe 1990, del Hoyo et al. 1994), we did not observe soaring flights or aerial displays above the canopy during the breeding season at nest sites or while we conducted raptor surveys from 1988 to 1992 (Whitacre et al. 1992). The birds rarely soared above the forests in northeastern Guatemala, making detection extremely difficult during raptor censuses. In general, they appeared to move through and below the canopy rather than above it. We occasionally sighted individuals sitting on conspicuous perches above the canopy.

At one nest site both members of a pair were banded prior to egg laying in 1991. The female disappeared one week later and a new, unbanded female replaced the marked female. The first banded female was observed nesting the following breeding season (1992) on a neighboring territory, where she successfully fledged three young. This suggests that the

pair bond was not firmly established when the first adults were banded in 1991, and that there were unpaired individuals in the population. Unpaired, non-territorial individuals have been documented in other *Accipiter* populations (Newton 1986). In 1993, we recorded one instance of bigamy or extra-pair copulations at one nest site. The intruding male did not appear to have a detrimental effect on the reproductive success of this pair.

The breeding cycle was approximately 188 days from nest building to dispersal of young from their natal areas (February to July). This is comparable to the tropical Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*; 184 days), also having a relatively long breeding period (Delannoy and Cruz 1988), which is longer than the Cooper's Hawk in Oregon (132 days) and European Sparrowhawk (*Accipiter nisus*) in Scotland (110 days; Reynolds and Wight 1978, Newton 1986, Delannoy and Cruz 1988). As with the Puerto Rican Sharp-shinned Hawk (Delannoy and Cruz 1988) and the Bicolored Hawk (Mader 1981) in Venezuela, the extended period between occupancy of nesting sites and initiation of laying accounted for the differences in the duration of breeding cycles. The longer breeding period of the Bicolored Hawk compared to the Cooper's Hawk (Millsap 1981, Reynolds and Wight 1978) resulted from early nest building and courtship activity in February, egg laying in April, and a longer fledgling period.

Bicolored Hawks at 17° N latitude in Guatemala constructed nests early in the dry season. Incubation and nestling periods were during the dry season with fledging occurring at the start of the next wet season. In Venezuela, Mader (1981) suggested that raptors might occasionally nest during both wet and dry seasons. Mader (1981) found one pair of Bicolored Hawks constructing a nest in May at the start of the rainy season and fledging young in July. Another pair was observed nest building in May, the start of the rainy season in Venezuela at 6° N (Mader 1981). We suggest that the reason for the variation in timing of the breeding cycle between these two sites is related to local food availability. This difference in the timing of breeding between Guatemala and Venezuela may be caused by the response of different habitats to rains, which

might affect the availability of avian prey and ultimately the nesting period of these bird-eating hawks. In Guatemala, young Bicolored Hawks fledged June–July when many species of prey birds also fledge their young.

Food habits.—Reports on diet are few and mostly of hawks taking thrush to pigeon sized birds (Brown and Amadon 1989) and some lizards (Stiles and Skutch 1989). In Venezuela, a Squirrel Cuckoo (*Piaya cayana*; Mader 1981) and a mockingbird (*Mimus gilvus*; Friedmann and Smith 1955) were taken by Bicolored Hawks. The most complete record of prey comes from Peru where 13 birds and 1 squirrel were observed captured or carried as prey (Robinson 1994).

In Guatemala, Bicolored Hawks delivered mainly birds to their nests, but some reptiles and mammals were also recorded as prey. With a 95% avian diet in our sample, the Bicolored Hawk was the preeminent bird-eating specialist at Tikal. Only two other species demonstrated an equivalent reliance on birds: the Bat Falcon (*Falco ruficularis*; Parker 1997), which takes much smaller birds above or within the upper canopy or within openings in the vegetative cover, and the Orange-breasted Falcon (*F. deiroleucus*; Baker 1998), which also takes mainly flying prey above the forest. The two forest-falcon (*Micrastur* spp.) species at Tikal relied substantially less on avian prey, with the large Collared Forest-Falcon (*M. semitorquatus*) taking many mammals. Barred Forest-Falcon (*M. ruficollis*) took many small, arboreal lizards, in addition to avian prey (Thorstrom 1993).

Nest-site characteristics.—Nest trees of Bicolored Hawks were situated in low-canopied bajo forests, transitional forests, and high-ground forests. We speculate that Bicolored Hawks may select these habitat types with their relatively open canopy for easier access to the nest, fewer connections between neighboring trees (more isolated emergents), which would limit movements of arboreal animals, and possibly a lower density of terrestrial predators.

This *Accipiter* is reported to occupy a variety of habitats with no apparent specialization. Bicolored Hawks have been reported to occupy second-growth and even palm savannas with gallery forest, but they appear to be more common in drier or open forests, park-

land, forest edges, and rain forests (Fjeldså and Krabbe 1990, del Hoyo et al. 1994). Nest site locations in the bajo and hill base forests possibly provide some protection against nest predators. The low canopied bajo forests appear to limit spider monkey (*Ateles geoffroyi*) activity, possibly reducing the potential for these primates to prey on Bicolored Hawk nests. We observed Bicolored Hawks aggressively defending their nests from spider monkeys and predatory birds, such as Ornate Hawk-Eagles (*Spizaetus ornatus*), Keel-billed Toucans (*Ramphastus sulfuratus*), and Brown Jays (*Corrocoryx murio*).

Breeding density.—Based on home range estimates and breeding densities Bicolored Hawks in Tikal National Park occupied 4.0–5.5 km² per territorial pair. Territories were evenly spaced throughout the study area even though Bicolored Hawks were somewhat specific in their nesting requirements for bajo and transitional forests. In a 100 km² area, we estimate that the breeding density would range from 18 to 25 territories assuming suitable habitat was available. In French Guinea, Thiollay (1989) estimated that the breeding density for this species was 4 territorial pairs per 100 km² or 25 km² per pair, 5 times less dense than our estimate. We suspect that a difference in the forest habitat, relatively dry (Tikal National Park) versus wet (French Guiana) tropical forests, may contribute to this large difference. We also speculate that our estimates may reflect the more accurate estimate of the species' breeding density because Thiollay (1989) did not use neighboring territories to estimate Bicolored Hawk densities.

Productivity.—The reproductive output was low during the study with 1.4 young fledged/breeding attempt. Although the reproductive rate was somewhat low, the nesting success was high with an average of 76% of all nesting attempts resulting in successful fledglings. Thus, if a pair of Bicolored Hawks was successful in laying eggs they had a good chance of successfully producing offspring. The Bicolored Hawk population in Tikal appears to be stable and density-dependent.

Production and nesting success was higher for the Bicolored Hawk than for the insular congeneric Puerto Rican Sharp-shinned Hawk (Delannoy and Cruz 1988). The Puerto Rican Sharp-shinned Hawk suffered a higher degree

of nest failures from nestling mortality attributed to parasite infestation and desertion of clutches, neither of which were observed in Bicolored Hawks at Tikal National Park. Bicolored Hawks at Tikal National Park were secretive bird-feeding specialists and appeared to be evenly spaced throughout the forest, suggesting that breeding densities were limited by territorial behavior in a density-dependent fashion (Newton 1979). These raptors have a breeding biology and behavior that follows the general strategy of other tropical forest birds. These adaptations include a lower reproductive output, high adult survivability, and a protracted breeding season in comparison with Temperate zone raptors (Newton 1979, 1986; Delannoy and Cruz 1988). We verified that this species has the ability to re-nest if nest failure occurs early in the breeding cycle. Bicolored Hawks had a lower predation rate than cavity-nesting Barred and Collared forest-falcons at the same study site (Thorstrom 1993). Our results support the view that tropical environments tend to select for reduced natality as a life history strategy.

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